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Stability Analysis of Agronomic Traits in Potato Cultivars of Different Origin

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Abstract Potato (*Solanum tuberosum* ssp. *tuberosum*) cultivars are expected to express a stable level for traits important for growers and consumers. To investigate how this expectation was met by a set of 21 cultivars bred in Hungary, Poland and Spain, 2-year field experiments were carried out in these countries for the evaluation of tuber yield, starch content and yield, and occurrence of secondary growth of tubers. Stability in an agronomic sense was evaluated by the analysis of genotype by environment interaction (GE) using the Scheffé-Caliński mixed model. Unstable trait expression was indicated by the statistically significant share of GE in the variability contributed by a specific cultivar. This instability could lead to either complete or partial unpredictability. Stable trait expression was observed for 6–11 cultivars, depending on the trait. A significant genetic factor, which indicates broad adaptation, was rarely found. Stable expression of tuber yield occurred together with stable or predictable expression of both starch content and yield. Unstable expressions of tuber and starch yield were also associated. The stability or instability of secondary growth was not associated with stability or instability of the other measured traits. Analysis of GE interaction was useful for identifying stable or unstable responses and revealed the presence of incomplete stability or partial unpredictability as intermediate types of reaction.

Resumen Se esperaría que las variedades de papa (*Solanum tuberosum* spp. t*uberosum*) expresen un nivel estable de caracteres importantes para productores y consumidores. Para investigar como esta expectativa pudiera darse en un juego de 21 variedades de Hungría, Polonia y España, se llevaron a cabo experimentos de campo durante dos años en estos países para la evaluación de rendimiento de tubérculo, rendimiento y contenido de almidón, y la presencia de crecimiento secundario de tubérculos. Se evaluó la estabilidad, en un sentido agronómico, mediante el análisis de la interacción genotipo-medio ambiente (GE), usando el modelo de la mezcla Scheffé-Caliński. La expresión de un carácter inestable se indicó por la significancia estadística de GE en la variabilidad proporcionada por una variedad específica. Esta inestabilidad podría conducir ya fuera para imprevisibilidad completa o parcial. La expresión de un carácter estable se observó en 6–11 variedades, dependiendo del carácter. Raramente se encontró un factor genético significativo que indicara amplia adaptación. La expresión estable de rendimiento de tubérculo se presentó junto con la expresión estable o predecible tanto con el contenido como con el rendimiento de almidón. También se asociaron expresiones inestables de rendimiento de tubérculo y almidón. La estabilidad o inestabilidad de crecimiento secundario no se asoció con estabilidad o inestabilidad de los otros caracteres medidos. El análisis de la interacción GE fue útil para la identificación de respuestas estables o inestables y reveló la presencia de estabilidad incompleta o imprevisibilidad parcial como tipos intermedios de reacción.

Keywords G × E interaction · Scheffé-Caliński model · Tuber yield · Starch yield · Secondary growth of tubers

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Introduction

Among the major crops, potato (*Solanum tuberosum* ssp. *tuberosum*), with an annual production of 375 million tons (http://faostat.fao.org) is globally 4th, behind wheat, rice and barley. This economic importance stems from the many diverse uses of potato tubers for fresh, processing, and starch markets, or even as animal feed (Horton and Anderson 1992; Lisińska 2006). In 2011, the average tuber yield in the world was equal to 19.4 $t{\cdot}ha^{-1}$; in European Union countries this varied from 10 $t{\cdot}ha^{-1}$ to 50 $t{\cdot}ha^{-1}$ (http://faostat.fao.org), while under optimal experimental conditions it may reach 120 $t{\cdot}ha^{-1}$ (MacKay 1996). This indicates the great adaptability of potato and its high yield potential, but also the large role of genotype × environment interaction (GE).

The most desired type of cultivar is one that combines high yield with stability in a dynamic (or agronomic) sense (Eberhard and Russel 1966; Piepho 1996). In this sense, the cultivar response to environmental factors is parallel to the mean response of all cultivars, which are tested in different environments. Detailed insight into the contribution of each genotype/cultivar (G) and environment (E), i.e. location (L) by (Y) interaction, to the overall GE interactions has been facilitated by developing statistical methods (Becker and Leon 1988; Cooper and DeLacy 1994). According to Gauch (2006), for scientists dealing with plants, including plant breeders, the main effect of G concerns broad adaptation, whereas GE interaction concerns narrow adaptation. For farmers, growing cultivars with stable yield (i.e. with large G effect and small GE) results in a larger harvest and enhanced competitiveness in the market place.

The objective of this research was to test performance and stability of yield, starch content and its yield, and the occurrence of secondary growth of tubers in various environments. The set of 21 cultivars was tested in field trials. These cultivars were of Polish, Hungarian and Spanish origin and were described as table stock (with one exception) with very high, high or good yielding potential in the countries of their origin. In order to distinguish cultivars with stable expression of traits and to examine possible differences in stability, analysis of GE interactions was undertaken. Environments were represented by three significantly different locations in Poland, Spain and Hungary, in which trials were performed during 2 years.

Materials and Methods

Cultivars

From among 22 cultivars tested in field trials, 8 entries (Bartek, Benek, Elanda, Finezja, Niagara, Sekwana, Tetyda, Zagłoba) were developed in Poland at the Potato Breeding Zamarte Ltd., Co., 8 entries (Demon, Goliat, Hopehely, Katica, Lorett, Rioja, Venusz Gold, White Lady) came fromHungary and were bred at the Potato Research Centre of Pannonia University and 5 were of Spanish origin. Spanish cvs Gorbea, Irati and Leire were bred by The Basque Institute of Agricultural Research and Development, Neiker-Tecnalia, and cvs Jimena and Nela by Appacale S.A.. Most cultivars in this set were mid-early in maturity with the exception of Niagara and Sekwana (mid-late) and Zagłoba (late). The cultivars were table stock with the exception of Sekwana (starch). However, Finezja, Irati and Jimena are suitable for processing. Most of these cultivars were resistant to potato virus Y and Ro1 pathotype of nematode *Globodera rostochiensis*. Dutch cv Desiree served as a control, for which seed tubers were provided to other participants by the Spanish partner.

Site Description and Experimental Design

The field trials were conducted at three locations in central Poland (POL), in central Hungary (HUN) and north-western (Galicia region) Spain (ESP) in two subsequent years 2008 and 2009. HUN is characterized by a continental climate, POL as oceanic with continental climate influences and ESP as an oceanic climate without seasonal drought. Precipitations and temperatures varied greatly among environments (Fig. 1).

Trials were performed on sandy soil plots. Fertilizers were applied on the basis of soil analysis and their doses were as follows: a) 92 kg N ha^{-1}, 75 kg P_2O_5 ha^{-1} and 190 kg K_2O ha^{-1} in POL; b) 180 kg N ha^{-1}, 160 kg P_2O_5 ha^{-1} and 300 kg K_2O ha^{-1} in HUN; c) 90 kg N ha^{-1}-, 180 kg P_2O_5 ha^{-1} and 270 kg K_2O ha^{-1} in ESP. Full chemical protection of plants was applied. Whole tuber seeds were planted at a spacing of 75 cm (HUN and ESP) or 67.5 cm (POL) in the last week of April with the exception of the ESP2009 trial, which was planted on the 4 May. Tubers were harvested in mid-September or early October (HUN2008).

The experimental design was a randomized complete block. In each of 3 blocks, cultivars were planted in 60 hill plots. Data collected from each plot were: (a) total tuber yield (kg $plot^{-1}$), (b) starch yield (kg $plot^{-1}$), (c) starch content (%) and (d) proportion of tubers with secondary growth.

Statistical Analysis

The data were analyzed in two steps. The first step was a classical one-way ANOVA for each trait to determine differences among cultivars in each of the six field experiments (3 locations (L)×2 years (Y)). The arcsine transformation was applied to the proportion of tubers with secondary growth.

Secondly, data from the six environments were combined and analyzed using SERGEN version 3 software (Caliński et al. 1998). This program is based on the Sheffe-Caliński mixed model (Scheffe 1959; Caliński 1966; Mądry and Kang

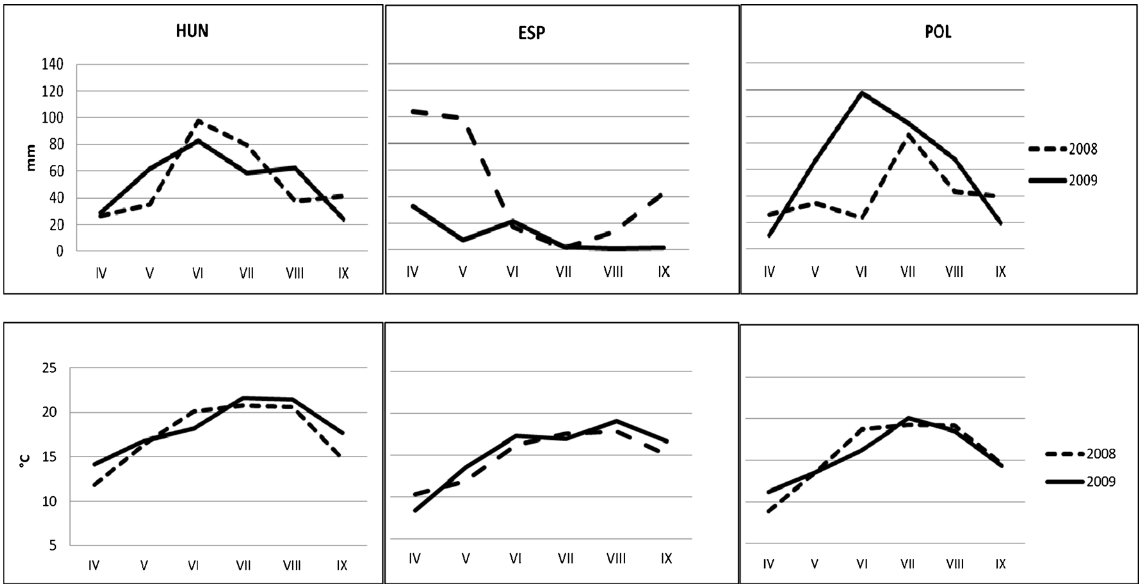

Fig. 1 Precipitation (in mm) and temperatures (in °C) in months from April to September in years and locations

2005) and the Caliński-Kaczmarek joint regression model (Kaczmarek 1986; Caliński et al. 1997; Mądry and Kang 2005). The model was previously described and utilized by Tatarowska et al. (2012).

The combined analysis of variance evaluates the influence of cultivar (G), environment (E) and GE effects on examined traits. Each environment was a combination of year × location. The significance of cultivar (main), as well as interaction effects, in the variation contributed by each cultivar were evaluated. Thus, for each cultivar two basic parameters were tested: main effect and effect of the highest order GE interaction. Joint regression analysis was performed to determine whether and to what extent the regression explained GE interaction.

Finally, accordingly to the model proposed by Scheffé-Caliński, canonical variables analysis (CVA) was performed to describe GE effects. Essentially, this method is similar to principle component analysis. The difference is that CVA is based on F-statistic values rather than the observed values used in principal components. The results of CVA are presented in biplots, which simultaneously show environments and cultivars in a coordinate system of the first two canonical variables. In biplots, environments are represented by vectors (half-lines) and each cultivar by a point, whose coordinates are determined by values of only these two canonical variables. In the majority of cases, points lying close to the origin indicate cultivars with insignificant GE interaction, i.e. cultivar points within the oval. For points outside the oval, the perpendicular projection of points to the vector or half-line determined by extending vector representing a given environment identifies cultivars for which positive GE effect on a trait in a given environment was found. This effect increases with decreasing distance between specific point and the half-line.

Results of combined ANOVA are presented for tuber yield, starch content and its yield and secondary growth of tubers. However, detailed tabular presentation of analysis of GE interaction is limited to tuber yield. For other traits, results of such analyzes are given in summary table and biplots.

Results

Cultivars Differentiation in Environments

Mean values of measured traits are presented in Table 1. Preliminary one-way ANOVAs (not presented in the table) showed that in each environment there were highly significant differences among cultivars (P=0.01) for all traits with three exceptions: there were significant differences (P=0.05) among cultivars for starch content in 2009ESP and tuber secondary growth in 2008ESP; and, no significant differences among cultivars for tuber secondary growth in 2009ESP.

Total Tuber Yield (TTY)

Combined ANOVA for total tuber yield revealed significant effect of E, G and GE interaction (Table 2). The E, G, and GE sources of variation accounted for 9 %, 8 % and 6 % of the total sums of squares (SS) respectively, but the most important effect was that caused by location (L accounted for 58 % of SS).

In the analysis of GE interaction, the estimates of the cultivar main effect indicated that tuber yield was significantly higher in Finezja (P=0.05) and significantly lower in Jimena (P=0.01) (Table 3).

Table 1 Mean values of examined traits in environments, years and locations

Trait	Environment						Year		Location			General mean
	2008POL	2008HUN	2008ESP	2009POL	2009HUN	2009ESP	2008	2009	POL	HUN	ESP	
TTY (kg/plot)	76.36	68.36	31.80	77.77	67.82	55.74	58.84	67.11	77.06	68.09	43.77	62.98
STA (kg/plot)	11.17	10.35	4.22	10.92	10.71	8.03	8.58	8.92	11.05	10.53	6.13	9.23
SC (%)	14.76	15.21	13.24	14.10	15.87	14.43	14.40	14.80	14.43	15.54	13.83	14.60
SEC	0.29	0.29	0.23	0.14	0.13	0.09	0.27	0.12	0.21	0.20	0.15	0.19

TTY total tuber yield, *STA* starch yield, *SC* starch content, *SEC* fraction of tubers with secondary growth

The GE interaction was significant for 12 cultivars, but for only 4 of them was this interaction explained by regression of GE on E (significance at P=0.05 or P=0.01 and R^2>90 %) (Table 3). For some cultivars, other types of interactions were found to be significant, namely the interactions GY and GL (Finezja) and GL (Desiree and Jimena). No significant GY, GL or GE interactions were found for 7 cultivars (Tables 3 and 4).

Starch Yield (STA)

The combined ANOVA revealed significant E and GE interaction (P=0.01), which accounted for 10 % and 6 % of SS respectively. However, the most important effect was that caused by location, which accounted for 58 % of the SS (Table 2).

The data on significance of main effects and interactions are summarized in Table 4. Starch yield was significantly higher than the overall mean in Finezja and Venusz Gold, and significantly lower in Nela and Demon. For these cultivars, interactions were insignificant with the exception of Demon, for which GL was statistically significant. For the other 13 cultivars, the only significant interaction was GE (at P=0.01 or P=0.05), which was explained by regression GE on E in the case of Elanda and Lorett (P=0.05 and R^2>90 %).

Starch Content (SC)

For starch content, all three major sources of variation, i.e. genotypes (G), environments (E), and GE interaction, were significant (P=0.01). In contrast to the other traits, a substantial portion of the total variation was attributable to G effect (55 % of the SS) (Table 2).

Starch content was significantly higher than the overall mean starch content in 4 cultivars and significantly lower in 4 cultivar (Table 4). In addition, the GE interaction effect was significant for 10 cultivars. For Nela and Katica, this interaction was explained by linear effects, since the regression was significant (R^2>0. 90). For Demon the only significant interaction was GL, which was also true for starch yield (Table 4).

Table 2 Mean squares (MS) variation and contribution in sum of squares (SS) for total tuber yield (TTY), starch yield (STA), starch content (SC) and fraction of tubers with secondary growth (SEC)

Source of variation	Degrees of freedom	TTY		STA		SC		SEC	
		MS	% of SS	MS	% of SS	MS	% of SS	MS	% of SS
Year (Y)	1	2256.96	5 %	56.37	5 %	5.16	1 %	33.28**	19 %
Location (L)	2	13054.46	58 %	321.56	58 %	32.95	13 %	1.89	2 %
Environments (E)	2	2037.16**	9 %	52.81**	10 %	9.95**	4 %	0.13	0 %
Genotypes (G)	21	168.21**	8 %	2.91	5 %	13.57**	55 %	1.68*	20 %
G × Y (GY)	21	28.71	1 %	0.84	2 %	0.62	2 %	0.66	8 %
G × L (GL)	42	100.75	9 %	2.39	9 %	1.09	9 %	0.66	15 %
G × E (GE)	42	60.12**	6 %	1.68**	6 %	1.17**	9 %	0.85**	20 %
Regression on E	21	91.08		1.99		1.02		0.86	
Regression deviation	21	29.16**		1.37**		1.33**		0.84**	
Experimental error	216	8.87	4 %	0.25	5 %	0.15	7 %	0.12	16 %

*Significant at the level P=0.05

**Significant at the level P=0.01

Table 3 Analysis of GE interaction for total tuber yield

Cultivar	Main effect		Interactions				
	Estimation	F-statistic	F-statistic for			Regression of GE on E	
			GY	GL	GE	Coefficient	R^2
Tetyda	7.31	2.93	0.13	5.23	12.91**	−0.846	60.60
Niagara	6.23	1.84	0.81	0.03	14.92**	−1.141*	95.46
Lorett	5.90	2.62	0.33	2.48	9.41**	−0.926**	99.70
Zagłoba	4.95	0.98	0.02	0.34	17.76**	1.062	58.35
Elanda	4.67	0.76	0.10	1.71	20.28**	1.361**	99.93
Gorbea	4.08	2.95	2.54	0.29	3.99**	0.484	64.35
Hopehely	2.77	1.87	2.82	2.02	2.90		
Finezja	2.40	28.27*	18.02*	108.28**	0.14	0.061	27.86
Bartek	1.16	1.51	0.02	4.54	0.63		
Benek	0.86	0.03	0.04	0.05	18.52**	1.182	82.43
Irati	0.79	0.03	0.07	0.08	16.63**	−1.197*	94.28
Leire	0.47	0.10	0.25	0.46	1.55		
Desiree	0.43	0.09	0.58	17.37*	1.52	0.312	69.75
Goliat	0.23	0.01	0.39	5.02	3.25*	0.096	3.08
Sekwana	−2.01	10.54	0.00	1.28	0.27		
White Lady	−2.06	0.41	0.18	0.37	7.37**	−0.712	75.11
Katica	−2.51	1.36	1.82	2.43	3.29*	0.078	2.05
Demon	−3.16	10.37	1.25	2.42	0.68		
Nela	−3.18	2.39	0.85	0.74	3.00		
Venusz Gold	−5.10	10.76	2.95	0.43	1.71		
Rioja	−8.37	7.87	1.49	0.36	6.30**	−0.017	0.05
Jimena	−15.86	87.38**	0.64	14.05*	2.04	0.143	11.00

Data in the table are sorted in order of decreasing main effect

*Significant at the level $P=0.05$

**Significant at the level $P=0.01$

Secondary Growth of Tubers (SEC)

The combined ANOVA showed that secondary growth was significantly affected by GE ($P=0.01$) and G ($P=0.05$). For this trait, a great portion of the total variation was attributable to Y, G and GE interaction (19-20 % of the SS for each effect) (Table 2).

The proportion of tubers with secondary growth was significantly smaller than the overall mean for Leire ($P=0.05$) and significantly higher ($P=0.05$) for Desiree. For Desiree all interactions were not significant. There were no significant GE interactions for Finezja, Goliat, Rioja, Tetyda and White Lady. For the other cultivars, GE or GL interactions were significant. GE interaction was explained by regression for only three cultivars (Jimena, Niagara, Irati) (Table 4).

Specific Effects of GE Interaction—Biplots

The environments were significantly different, even if only the precipitation data or average temperatures are taken into account (Fig. 1). However, CVA gave further insight into the structure of GE interactions. In the resultant biplots, the symmetric layouts of the half lines representing environments indicate their strong differentiation (Fig. 2a, b, c, d). The length of each half line corresponds to the contribution that particular environment made to the GE interaction, which was calculated as the percentage of sum of squares for GE. In the case of TTY, STA and SC, the environments 2009ESP and 2008ESP made the largest contributions to this interaction, which were 25.2 % for TTY, 20.2 % for STA and 22.5 % for SC. The smallest contributions were found in environments 2008POL and 2009POL, which were 11.7 % for TTY, 13.7 %, for STA and 11.7 % for SC (Fig. 2a, b, c). For SEC, the reverse was observed since the largest contribution to variation caused by GE was found for the environments 2008POL and 2009POL (22 % in each), while the smallest contribution was from 2008ESP and 2009ESP (Fig. 2d).

The location of a cultivar point in a biplot is determined by the amount of variation contributed by that cultivar to the GE

Table 4 Cultivars grouping in accordance with statistical significance of main and interactions effects, regression coefficients and value of R^2

Trait	Main effect [a]	Interactions						
		Not significant	Significant					
			GY and/or GL	GE	and R^2>70 % [b]		Explained by regression [b]	
					Positive	Negative	Positive	Negative
TTY	NS	Bartek, Demon, Hopehely, Leire, Nela, Sekwana, Venusz Gold	Desiree	Gorbea, Goliat, Katica, Rioja, Tetyda, Zagłoba,	Benek	White Lady	Elanda	Irati, Lorett, Niagara
	Positive		Finezja					
	Negative		Jimena					
STA	NS	Desiree, Gorbea, Hopehely, Leire, Sekwana		Bartek, Goliat, Irati, Jimena, Katica, Nigara, Rioja, White Lady, Zagłoba	Benek	Tetyda	Elanda	Lorett
	Positive	Finezja, Venusz Gold						
	Negative	Nela	Demon					
SC	NS	Desiree, Irati, Leire,	Demon	Bartek, Elanda, Goliat, Gorbea, Niagara, White Lady	Benek	Finezja	Katica, Nela	
	Positive	Jimena, Rioja, Sekwana, Venusz Gold						
	Negative	Hopehely, Lorett, Tetyda, Zagłoba						
SEC	NS	Finezja, Goliat, Rioja, Tetyda, White Lady		Bartek, Gorbea, Katica, Lorett, Nela, Sekwana, Venusz Gold	Hopehely, Zagłoba	Demon, Elanda, Benek,	Jimena, Niagara	Irati
	Positive	Desiree						
	Negative		Leire					

[a] *NS* not significant; significant (positive or negative) main effect at the level P=0.05

[b] regression coefficients were significant (positive or negative) at the level P=0.05, or insignificant (for R^2 >70 %)

interaction. Points located near the origin indicate cultivars with insignificant GE, although sometimes with significant GY and/or GL interactions. Furthermore, points located very close to the specific half-line indicate cultivars for which GE interaction has a positive effect on that trait. This effect decreases with increasing distance between cultivar point and half line. Such positive effects on TTY were observed for Gorbea and Zagłoba in 2008HUN, for White Lady in 2009HUN, for Niagara, Lorett and Irati in 2008ESP, for Tetyda in 2009POL, and for Goliat and Katica in 2008POL (Fig. 2a).

The distribution of cultivar points for STA was noticeably different than for TTY, which indicates that GE interactions affected these two traits differently (Fig. 2b). In some environments positive GE effects were observed, as for White Lady and Goliat in 2009HUN, for Bartek and Zagłoba in 2008HUN, for Niagara and Tetyda in 2009POL, for Lorett in 2008ESP, for Elanda in 2009ESP, and for Benek in 2008POL (Fig. 2b).

As for SC, clearly positive GE effects were observed for Katica, Nela and Benek in2008POL, for Elanda in 2009ESP, for Bartek and Niagara in 2008HUN, for Finezja in 2009POL, for Gorbea and Goliat in 2008ESP, and, for White Lady in 2009HUN (Fig. 2c).

For SEC, positive effects mean increases in the occurrence of this defect and those were observed for Elanda, Demon, Irati, Venusz Gold and Katica in 2008POL, for Lorett in 2009HUN, for Hopehely in 2008ESP, for Jimena, Nela, Zagłoba and Niagara in 2009POL, for Bartek, Gorbea and Sekwana in 2008HUN, and for Bartek in 2009ESP (Fig. 2d).

Discussion

Genotype-environment interaction for yield is a common phenomenon that has been demonstrated in multi-environment trials with a lot of species of crop plants (Fox et al. 1997; Kang and Kumar 2000; Mekbib 2003; Blanche et al. 2009) including potato (eg. Tai 1971; Mallory and Porter 2007; Mulema et al. 2008). The reaction of other traits of potato to changing environment has occasionally been examined (e.g. Tatarowska et al. 2012). In the case of potatoes, Bradshaw (1997) distinguished genotype-macroenvironment and genotype-microenvironment interactions. The macroenvironment represents locations, seasons and crop managements, while microenvironment is basically the equivalent of experimental error.

Cultivars were divided into those for which the GE interaction was significant, indicating unstable expression of individual traits, and, those for which the GE interaction was

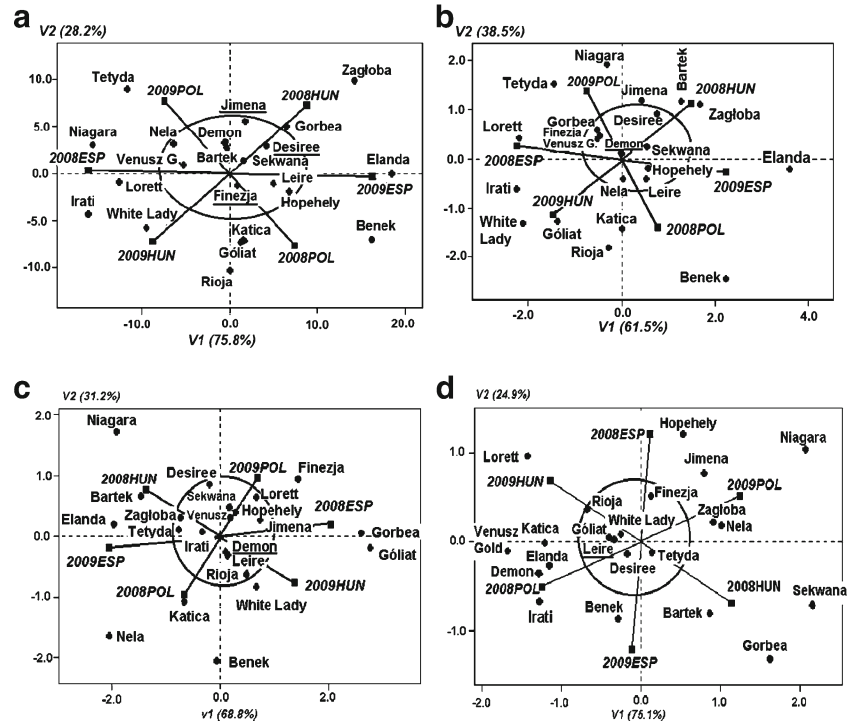

Fig. 2 Vector representation of 6 environments and 22 cultivars in the system of canonical variables V1 and V2 for **a** total yield of tubers, **b** starch yield, **c** starch content and **d** fraction of tubers with secondary growth. Within ovals—cultivars with insignificant GE interaction; cultivars with significant GY and/or GL are underlined

insignificant, indicating stable expression of individual traits. However, such a division seems to be a simplification, if the other parameters are not taken into account, i.e. the significance of main (cultivar) effect, presence of interactions other than GE and presence of linear component in GE interaction. The types of reaction to environment exhibited by cultivars are discussed further and recapitulated in Table 5.

Stability

Stable expression of traits is indicated by an insignificant GE interaction. Neither G nor GE were significant for tuber yield, starch yield, starch content, and secondary growth of tubers for 7, 5, 3, and 5 cultivars, respectively. Significant G, but insignificant GE were found for tuber yield, starch yield, starch content, and secondary growth for 0, 3, 8, and 1 cultivars, respectively.

Significant lower-order interactions (GY and/or GL) were found for a few cultivars of high (Finezja), medium (Desiree) and low yields (Jimena). Significant GL interactions were observed for starch content and yield in Demon and for the occurrence of secondary growth of tubers in Leire (Tables 4 and 5). However, Finezja has proven its value in terms of tuber yield (positive G) and Leire in terms of occurrence of secondary growth of tubers (negative G), whereas, Jimena has poorer tuber yield (negative G) and Demon has poorer starch yield (also negative G). Hence, significant GY and/or GL may indicate incomplete stability rather than instability.

The most desirable cultivar should exhibit stability combined with a significant and positive main effect, which indicates broad adaptation, i.e. the ability to achieve high levels of a given trait in the majority of environments (in the case of secondary growth of tubers, broad adaptation is indicated by a significant negative main effect). However, this was rarely observed. Broad adaptation in terms of tuber yield was found for Finezja. Leire was the only cultivar for which stable tuber yield was associated with stable low intensity of tuber secondary growth. Broad adaptation in terms of starch content could be important for starch or processing cultivars. However, for table stock, stable expression of good taste should be more essential. Starch content is but one of many factors determining cooking quality of tubers (Jansky 2010).

For occurrence of secondary growth the combination of insignificant GE with insignificant or significant negative main effects seems to be most desirable. Stable cultivars usually showed insignificant main effects: the exceptions were Desiree and Leire. The stable level of secondary growth of tubers in Desiree was disadvantageous because the defect was significantly higher than the overall mean (significant positive main effect). Leire was the only cultivar to have a significant negative main effect for occurrence of secondary growth, but this was associated with significant GL interaction, indicating incomplete stability (Tables 4 and 5).

The stable or incompletely stable expression of yield was usually associated with a similar expression of starch content and yield (Table 5). Starch yield is a complex parameter, which is usually maximized during breeding starch potatoes,

Table 5 Reaction to environment in tested cultivars

Cultivar	Expression of trait[a]			
	TTY	STA	SC	SEC
Sekwana	Stable	Stable	Stable	Unpredictable
Hopehely	Stable	Stable	Stable	Partially predict.
Leire	Stable	Stable	Stable	Incompl. stable
Venusz Gold	Stable	Stable	Stable	Unpredictable
Nela	Stable	Stable	Predictable	Unpredictable
Demon	Stable	Incompl. stable	Incompl. stable	Partially predict.
Desiree	Incompl. stable	Stable	Stable	Stable
Finezja	Incompl. stable	Stable	Partially predict.	Stable
Bartek	Stable	Unpredictable	Unpredictable	Unpredictable
Jimena	Incompl. stable	Unpredictable	Stable	Predictable
Lorett	Predictable	Predictable	Stable	Unpredictable
Elanda	Predictable	Predictable	Unpredictable	Partially predict.
Irati	Predictable	Unpredictable	Stable	Predictable
Niagara	Predictable	Unpredictable	Unpredictable	Predictable
Benek	Partially predict.	Partially predict.	Partially predict.	Partially predict.
White Lady	Partially predict.	Unpredictable	Unpredictable	Stable
Gorbea	Unpredictable	Stable	Unpredictable	Unpredictable
Tetyda	Unpredictable	Partially predict.	Stable	Stable
Katica	Unpredictable	Unpredictable	Predictable	Unpredictable
Rioja	Unpredictable	Unpredictable	Stable	Stable
Zagłoba	Unpredictable	Unpredictable	Stable	Partially predict.
Goliat	Unpredictable	Unpredictable	Unpredictable	Stable

[a] incompl. stable,- incompletely stable; partially predict., partially predictable

In italic—names of cultivars showing reaction of STA and/or SC, which is inconsistent with reaction of TTY (in terms of GE significance)

Underlined—broadly adapted cultivars (significant and positive main effect, with exception of SEC, for which the main effect is negative)

since selection for only high starch content may lead to a reduced tubers size and lower tuber yield (Ifenkwe and Allen 1978). In this study, starch yield was used to test how such a complex parameter is influenced by GE interaction.

Instability

An unstable expression of a trait occurs when statistically significant GE is found for a specific cultivar (Tables 4 and 5). However, this may take different forms. If the non-linear component was predominant in GE interaction, the reaction may be regarded as completely unpredictable in different environments. However, if the regression explained such interaction, the expression of the trait in different environments is predictable to some extent. Negative regression coefficients indicate that the cultivar performs better in less favorable conditions. In the case of tuber and/or starch yield, such cultivars may be called extensive types (Niagara, Lorett, Irati). On the other hand, positive coefficients indicate intensive cultivars, i.e. those performing better in better conditions (Elanda). Positive and negative regression coefficients were also found for starch content and secondary growth of tubers.

In addition, for a few cultivars the regression was insignificant, but R^2 was still high (≥70%), suggesting partially predictable expression of the trait. This was found for Benek (intensive) and White Lady (extensive) for tuber yield or Benek and Tetyda (both extensive) for starch yield. Similar partial predictability was found for two other traits (Table 4).

Absolute unpredictability was not a predominant type of reaction, since it was observed for 6–7 different cultivars in the case of tuber yield, starch content and secondary growth of tubers, and for 9 cultivars in the case of starch yield (Table 5). If tuber yield was stable or incompletely stable, the expression of the other two traits associated with yield, i.e. starch content and its yield, was usually stable, incompletely stable or at least predictable such as starch content in tubers of Nela and Finezja. Exceptions were found for Bartek and Jimena. Conversely, the various types of unstable expression of tuber yield were usually associated with different types of instability of starch yield, with the exception of Gorbea. But, unstable expression of tuber or starch yield went together with unstable or stable level of starch content (Table 5).

Tuber yield and starch content are polygenic traits, displaying continuous variation and environmental influence. The genetic variation of these traits was studied in numerous field experiments devoted to combining ability analyses (Bradshaw 2006). With the development of molecular genetics, a number of QTLs for tuber yield and starch content have been identified. It was found that most QTLs for yield were linked with QTLs for starch content. This suggests that the same genetic factors control both traits (Schäfer-Pregl et al. 1998). These findings may explain the observed coincidence of stable response to environment of tuber yield, starch content and starch yield. However, time to plant maturity and tuberization may also affect tuber yield, and starch content and yield (Schäfer-Pregl et al. 1998). These are related physiological traits controlled by genetic factors and day length. These genetic factors have pleiotropic effects on tuberization, plant maturity, tuber yield and starch content. Taken together polygenic inheritance, pleiotropic and environmental effects, and particularly day length, it may be concluded that some cultivars may be more sensitive to environmental factors and less stable in yield and starch content.

The occurrence of secondary growth of tubers was predominantly unstable, being found in 15 cultivars. However, for 8 cultivars different levels of predictability were noted. If such predictability was indicated by a significant and negative coefficient of regression, the cultivar shows low intensity of secondary growth in conditions favorable to the formation of this fault, but a higher level in environments less conducive to this defect. This was found for Irati and less clearly for Benek, Demon, and Elanda (Table 4).

Environmental factors promoting the secondary growth of tubers have been known for a long time (Lugt et al 1964), in contrast to the genetic components of this defect. Secondary growth is included among traits which would render tubers unmarketable and is intermittent in expression. Low (Dale and Mackay 1994) or moderate broad-sense heritability for this trait (Love et al. 1997) have been found. It indicates that potato breeding populations may have been selected against secondary growth (negative selection). Selection has to rely on observations in various environments over a number of years.

Conclusions

Field trials in this study were conducted in environments very different in terms of climate, weather and fertilization levels. Based on the analysis of GE interaction, a group of cultivars from different programs was found to be stable for tuber yield and related traits. Cultivars expressing stable low fractions of tubers with secondary growth were also found.

Although stable expression was observed for 6–11 cultivars depending on the trait, the genetic main effect was rarely significant. Hence, broadly adapted cultivars are very few.

A crucial point of this study is that stable tuber yield is usually associated with stable starch yield and content. However, unstable tuber yield is only closely associated with unstable starch yield, but not starch content. The practical consequence is that evaluation of tuber yield in different environments is sufficient for evaluation of stability of yield as well as its components.

Beside stable or unstable response, cultivars also exhibited incompletely stable reaction as well as unstable responses related to the various levels of predictability of trait expression. Such distinctions between unpredictable and predictable reaction may be useful for choice of cultivars accordingly to growing conditions, e.g. cultivars suitable for conventional or low-input cultivation system or for cultivation in areas with extremely changeable weather or on poorer soils.

Today potato breeders are able to conduct multi-environment trials to select individuals less sensitive to environmental changes. However, real progress in breeding potato cultivars exhibiting a stable level of yield and its components will be achieved if genetic factors controlling sensitivity to changeable environment are recognized.

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